EARLY STAGES OF ORB CONSTRUCTION BY *PHILOPONELLA VICINA*, *LEUCAUGE MARIANA*, AND *NEPHILA CLAVIPES* (ARANEAE, ULOBORIDAE AND TETRAGNATHIDAE), AND THEIR PHYLOGENETIC IMPLICATIONS

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ABSTRACT

The uloborid *Philoponella vicina* differs from the araneoids *Nephila clavipes* and *Leucauge mariana* in one movement made during frame construction, in the ordering of frame construction, in proto-hub removal, and in the highly ordered sequence of operations on adjacent radii just before proto-hub removal. Data from other uloborids suggest that all of these differences may distinguish orb weaving uloborids in general from orb weaving araneoids. *N. clavipes* differs from the other two species in the order of lines laid during frame construction, in the high variability in the details of frame construction, and in its failure to remove recently laid lines during exploration, radius construction, and frame construction. Frame construction behavior in all three species is more variable than previous reports indicated, and more variable than behavior in later stages of orb construction. In all three species earlier frame construction more often involves breaking lines already present in the web.

Similarity between uloborid and araneoid frame construction is more likely to be due to a combination of constructional constraints and inheritance of ancient spinning patterns than previously realized; it is not clear whether or not it constitutes a synapomorphy uniting the two groups. The failure of *N. clavipes* to remove recently laid lines during exploration, radius construction, and frame construction is probably plesimorphic. Secondary loss of removal behavior seems unlikely because removal probably confers adaptive advantages. Removal behavior in these contexts and possibly more stereotyped frame construction behavior probably evolved independently in uloborids and araneoids.

INTRODUCTION

The question of whether orb webs evolved once or more than once independently in uloborid and araneoid spiders has long been controversial (see Coddington 1986a and Shear 1986 for recent reviews, also Kovoor and Peters 1988). Perhaps the strongest evidence favoring the single origin hypothesis is that both the basic construction processes and the sequence in which they occur are similar in both groups (e.g., Wiehle 1927). Since similarities in later stages of orb construction could result from the patterns of lines produced during earlier stages, the earlier stages of orb construction are especially important for arguments of monophyletic origin. These stages, however, are the least studied and most poorly understood parts of orb construction behavior.

Part of the reason for our ignorance is that initiation of orb construction is more difficult to study than later stages: behaviors are not repeated as many times per web; lines and attachments are often displaced substantially by subsequent behavior (e.g., Tilquin 1942), making it difficult for an observer to maintain an accurate frame of reference; the spiders seem more sensitive to disturbances (Koenig 1951; Witt et al. 1968; Vollrath 1986); and construction of the first series of lines often involves long pauses (sometimes over an hour) (Witt et al. 1968). Arachnologists have had difficulty describing the early stages of web construction. For instance, there are many published descriptions of frame construction which are probably simply wrong (McCook, 1889; Hingston 1920; Comstock 1940; Savory 1952; Levi and Levi 1968; Dugdale 1969; Forster and Forster 1973; Levi 1978; Foelix 1982—see Tilquin 1942 and discussion of this paper); with the possible exception of Tilquin 1942, all other accounts (Peters 1933; Koenig 1951; Mayer 1952; Eberhard 1972; Coddington 1986a) are probably flawed in ignoring variations.

This paper reports detailed observations of the early stages of web construction by the uloborid *Philoponella vicina* (O. Pickard-Cambridge) and the tetragnathids *Leucauge mariana* (Kerserling) and *Nephila clavipes* (Linnaeus). It also gives brief descriptions of the behavior of four other uloborids, even briefer notes on that of a variety of other tetragnathids and araneids, and summarizes all published observations of certain aspects of uloborid behavior which appear to be unique to this group. The impact of these data on the single vs. multiple origin of orb controversy is then discussed.

METHODS

P. vicina and *N. clavipes* normally build between midnight and 0800 hours, so adult females of *P. vicina* and nymphs of *N. clavipes* (probably 2nd-6th instars) were kept in a small light-tight shed (about $3 \times 3 \times 2$ m) in which lights were turned on at 1400 hours and shone until 0500. A partially shaded 50 W bulb was kept burning at all times in order to increase the spiders' tolerance of light during the dark phase (Eberhard 1972).

Webs of *P. vicina* in the field were taped to a 25 cm diameter wire hoop; with the spider still in place, each was suspended horizontally in the shed. The spiders' behavior was observed as they built subsequent webs in the hoops. *N. clavipes* were induced to build webs on wire frames, which varied from 20-40 cm in diameter according to the size of the spider, by isolating the spider from contact with other surfaces by placing the frames in covered pails containing a little water. Both species were observed by lighting the background with a headlamp and watching their silhouettes, by shining the headlamp on the spider from the side and above, or by watching the spider against a surface illuminated by the 50 W bulb. Except when the headlamp shone upward from less than about 20 cm below the spider (a position avoided during the observations), it seldom caused overt disturbance of the spider (as indicated by interruption of building, bouncing on the web, or clear disorientation of behavior).

Observations of *N. clavipes* were especially difficult to record because the spiders' behavior was highly variable, so they were recorded verbally on a tape recorder, then later transcribed. To avoid startling the spider when I began to speak, a radio was played softly during the entire building period.

Mature female *L. mariana* were kept on horizontal wire hoops in an outdoor screen cage as described in Eberhard 1987a, and were observed late in the morning and early in the afternoon while they made their second complete webs of the day. These spiders moved much more rapidly, but their large size and the better viewing conditions made detailed observations possible.

The starting point of construction was standardized by cutting away most of the previous web that was present at the beginning of an observation period, using a scissors or a hot, fine-tipped soldering iron to leave only three long radial lines diverging from the web's previous hub. The mesh lines of *N. clavipes* outside the plane of the orb were generally left more or less intact. To assure that *P. vicina* and *L. mariana* webs were horizontal, any lines that the spider laid out of the plane of the hoop were cut just after they were laid.

My observations were somewhat prejudiced against unusual behavior patterns, because I was unable to record behaviors in which I did not understand the sequence of line placements and removals; "standard" patterns were easiest to understand because I could anticipate the spider's movements. The number of "standard" behaviors I recognized increased during the study, and toward the end I was seldom unable to understand any *P. vicina* aor *L. mariana* behavior. However, mesh construction by *N. clavipes* was so variable and complex that I was often unable to describe a spider's behavior, even at the end of the study. Orb construction in this species was much more stereotyped than mesh construction, but was still substantially more variable than that of the other species, and new sequences were seen even at the end of the study.

Construction of over 60 *P. vicina* webs, 60 *L. marina* webs and 35 *N. clavipes* webs was observed (6 of the *N. clavipes* webs were small "resting" webs without sticky spirals). Because I did not note all aspects of building behavior for each web, separate sample sizes are given for each behavior. In the latter part of the study I recorded complete lists of the directions and orders of placement of frames and radii in 17 *P. vicina* and 18 *L. mariana* webs, starting observations soon after the spider began sustained activity. These webs are called "study" webs in the text. The order of the spider's operations in each of these webs was later coded by counting back from the last radius laid in the web; in *P. vicina* I also counted the number of behaviors before and after proto-hub replacement. The position of a given behavior in the entire sequence is indicated in relation to the total number (N) of radii laid in the web (i.e., the last radius is $1/N$, the next-to-last is $2/N$, etc.). These fractions probably make some behaviors appear to have occurred earlier in the construction sequence than they actually did, since the totals do not include very early behaviors that were followed by long pauses.

The behavior of *Uloborus trilineatus* (Kerserling) was observed as in *P. vicina*, while all other species were observed in the field.

Unless otherwise noted, all statistical tests were made with Chi-squared Tests. Averages are followed by ± standard deviations. The figures which describe behavioral sequences are stylized summaries, and are not to scale. The behaviors observed are classified (e.g., radius construction, frame construction, mesh construction) on the basis of the web lines which were laid as a result of the behavior. Hub construction consisted of laying more or less circular lines at the hub which were attached to all or nearly all of the radii that were crossed.

Figure 1.—Web of *Philoponella vicina*: A, nearly complete proto-web; B, closeup of the proto-hub, showing large accumulation of loose silk and lack of hub lines connecting radii.
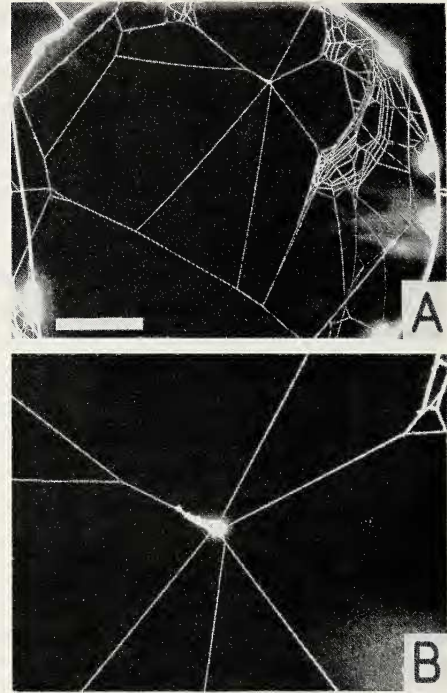
RESULTS

Philoponella vicina.—The following sequence summarizes the early stages of web construction. Initial "exploration" changed more or less gradually into construction of the radii and frames of the proto-web (Fig. 1). Then the spider always removed the center of this web ($N = 37$) (proto-hub removal or PHR) reconnecting the radii as it did so (Fig. 2). Following PHR, the spider began laying hub spiral, and laid more radii and sometimes more frames. These stages are described in detail below.

1. Exploration: The earliest portions of behavior, corresponding to the "exploration" stage of Eberhard (1972), were especially difficult to observe and describe, and I was unable to perceive overall patterns. Several details were the same as those of *U. diversus* (Eberhard 1972). Descents occurred both on the end of a single line, and while the spider spanned a broken line with its body, reeling in one broken end while paying out dragline silk that was attached to the other. Often descents on broken lines began with the spider paying out line faster than it reeled it in, and ended with it reeling in more rapidly than it paid it out. This caused the spider to descend through an arc, then climb more or less straight up. Some descents on single lines were preceded by two to four increasingly deep descents back and forth on the same radial line, but others were not. Spiders sometimes descended >50 cm to touch the floor, then immediately reascended the dragline without making an attachment. The failure to attach suggests that this behavior functions as exploration. Spanning lines carried on air currents (Eberhard 1987b) were often initiated on descents, but spiders did not usually move far from the original website.
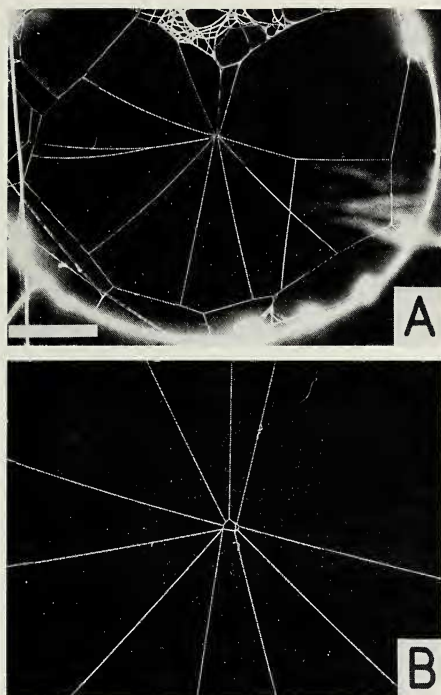
Figure 2. Web of *P. vicina*: A, just after proto-hub replacement (one radius was laid after the protohub was removed); B, closeup of hub of this web. The loose silk is gone, and the radii are connected by an approximately circular line that was laid as the loose silk was removed.

Spiders moved lines by breaking them at one end, and spanning the hole while carrying the broken end to another attachment site (Eberhard 1972). Similar results were achieved by removing a line entirely and replacing it with a new dragline that was attached at a different point. Accumulations of silk from previous webs were sometimes cut free and discarded with waving movements of legs I; other accumulations were cut free, wrapped for several minutes, and ingested as described for *U. diversus*. The reason some silk was discarded is unclear. Two spiders which dropped an accumulation of silk while removing lines from previous webs later ingested turfts of newly laid silk at the proto-hubs of the same webs.

The length of time spent in exploration varied greatly, and activity was often interrupted by pauses of an hour or more. Eventually several lines were joined together approximately where the future hub would be (the "proto-hub") (Fig. 2). Sometimes there were two such sites of intersection, and one was later removed or moved and added to the other.

Attachments to the wire rim were generally made on a surface of the wire that faced somewhat away from the direction of the line itself. This probably results in a firmer attachment to the substrate, since (other things being equal) the force exerted by the line on the attachment will be more nearly parallel to the plane of the attachment (compare the difficulty of pulling an adhesive tape directly off of a surface versus sliding it along the surface).

II. Frame construction and events leading up to PHR: The behavior immediately preceeding PHR became less variable. Radial lines were "modified" in one of three ways: moved; removed partially or completely; or connected by frames. Two kinds of partial replacements occurred. In the simplest and most common (124 of 126 cases in which this detail was recorded in the study webs),
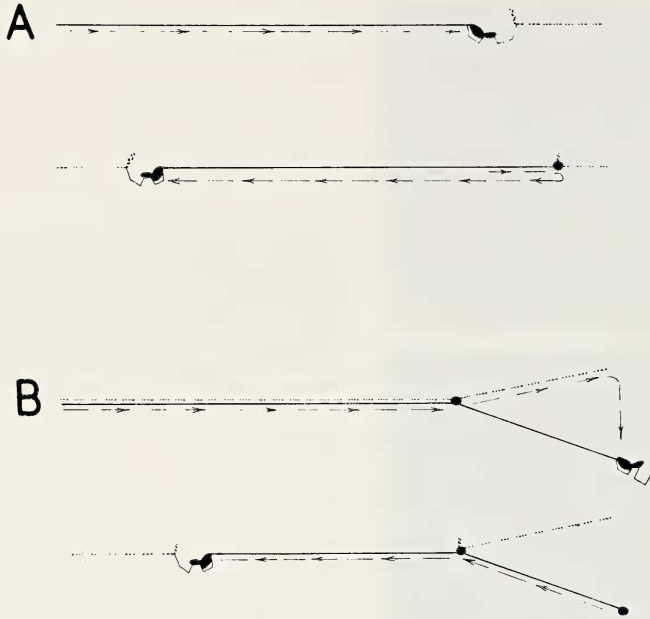
Figure 3.—Two types of partial replacement of radii: Dashed lines with arrows show the route taken by the spider's feet, dotted lines are lines already present, intact lines are those newly laid in each drawing, and large dots mark new attachments. A, the spider breaks and reels up the exit radius while moving away from the hub (above), then turns and replaces the newly laid dragline by breaking and reeling on the way back (below); B, the spider leaves the exit line intact as it leaves the hub, attaches its dragline to the exit on the way out and then moves onward and sideways (above). After making an attachment to the substrate or other lines, it returns, replacing the newly laid dragline and its attachments to other lines with another dragline and attachments (below).

the spider broke the exit radius while moving away from the proto-hub as just described. It stopped part way out the exit, turned 180° and attached the dragline to the outer broken end, then returned to the hub reeling up the dragline it had just laid (Fig. 3A). In a few cases (2 in the study webs) the exit radius was left intact on the trip out, the dragline was attached to it part way out and the spider continued onward and to the side without breaking the exit line (in one case it broke other lines it encountered there). After attaching the dragline, the spider returned to the hub, reeling up and replacing both the exit line and the line that it had laid on the way out (Fig. 3B).

Spiders also often moved radii by replacing them (56 of 186 cases in which radii were modified in study webs; 63% of the 56 involved frame construction). The spider began as if to replace the radius, breaking the line (the "exit radius") at the proto-hub or while moving away from the proto-hub and rolling up the loose silk as it went. It moved all the way to the end of the exit, then moved to one side along other lines or the wire rim, sometimes cutting other lines in the vicinity and/or attaching the dragline one or more times to them. Then it attached the dragline and turned back to return along it to the proto-hub, reeling up and replacing the newly laid line. The spider attached the new dragline at the hub, but did not generally make any other attachments before leaving on another trip away from the hub.

Sometimes (8 times in 17 study webs) the spider added a new radius: it moved away from the proto-hub without breaking the exit line, and then moved to the
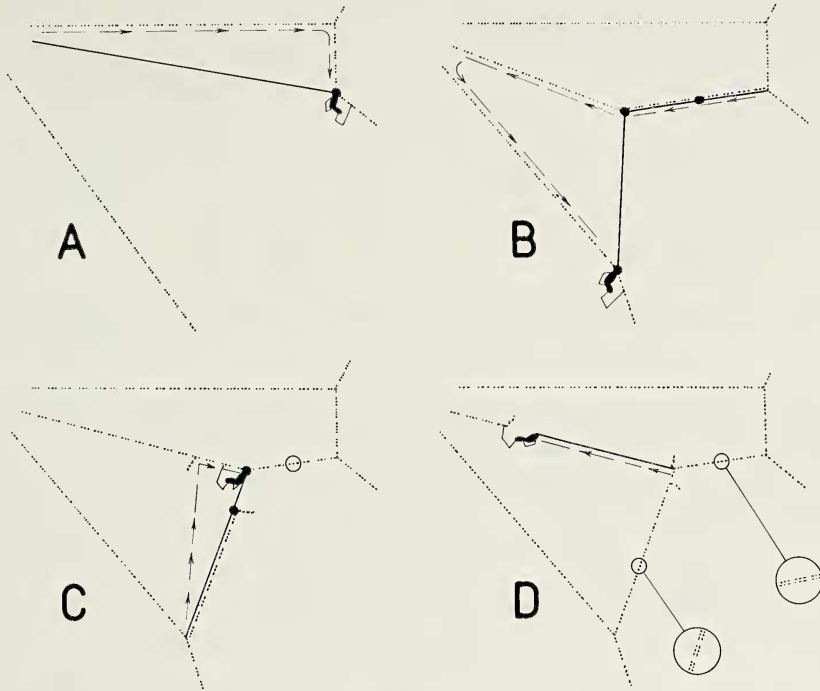
Figure 4.—Sequence of events in *P. vicina* frame construction Type A (conventions as in Fig. 3): Lines already present during a given stage are all represented as being single. Insets here and in later figures are included to clarify the number of "lines" actually present (in fact, spiders generally lay a pair or more of lines as they move; each line in the insets represents all of the components of a single dragline).

side, away from the end of this radius, attached its dragline to the frame line or wire rim, and returned to the hub along the new radius, breaking it and rolling it up as it went. This sequence of behavior was identical to the typical radius construction behavior of araneoids (F1 of Eberhard 1982). Addition of radii was probably more common than the numbers suggest since the very earliest stages of construction that were followed by long pauses were not counted. One radius (laid just before PHR) was sealed by the spider on its way to the hub (Fig. 8).

Frame construction behavior varied (types A-E in Figs. 4-8), but several details showed clear patterns. On the first trip back to the hub spiders sometimes attached to the exit radius twice instead of once as shown in Fig. 5B. Spiders always broke the second portion of the new frame line while returning to the new radius, and always shifted the attachment outward (e.g., Fig. 4C) before returning to the hub ($N = 126$) (Figs. 4-8). In four cases the new frame (e.g., the line laid in Fig. 4C) was slack and the spider reeled in part of the line with its legs IV, thus tightening it before attaching to the radius. The tuft of loose silk that accumulated as the spider returned from each frame construction and radius replacement was left along with other similar tufts at the proto-hub.

Frame construction behavior B (Fig. 5) was most common (44 of 70 cases in study webs); D (Fig. 7) was next (12 of 70), then A (Fig. 4) (9 of 70), C (Fig. 6) (3 of 70), and E (Fig. 8) (2 of 70). All A and B frame constructions occurred before PHR, all D came after PHR (D differs from A and B with respect to occurrence before or after PHR, $P < 0.01$); 2 of 3 C occurred before PHR).
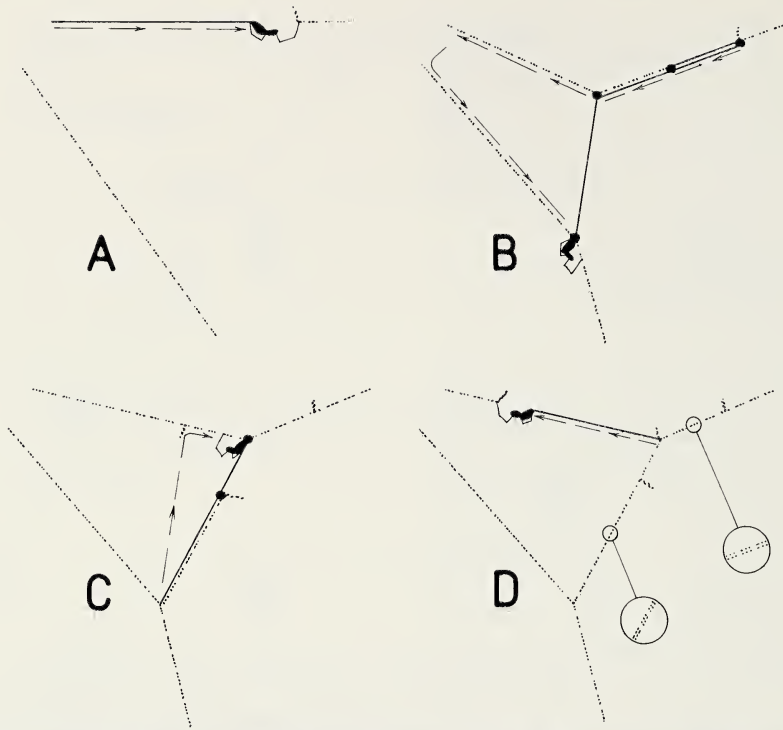
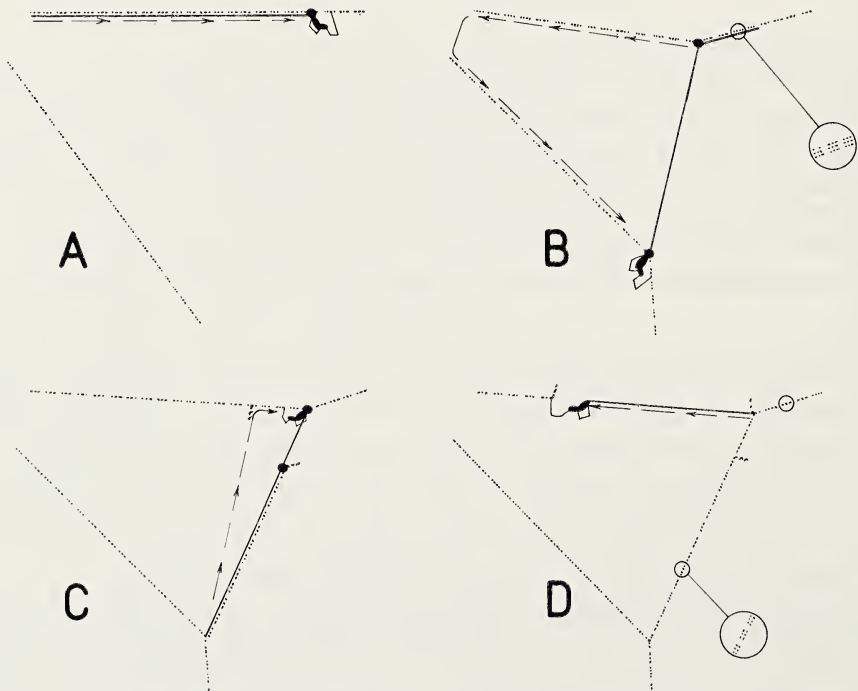Figure 5.—Sequence of events in *P. vicina* frame construction Type B (conventions as in Figs. 3 and 4).

Figure 6.—Sequence of events in *P. vicina* frame construction Type C (conventions as in Figs. 3 and 4).
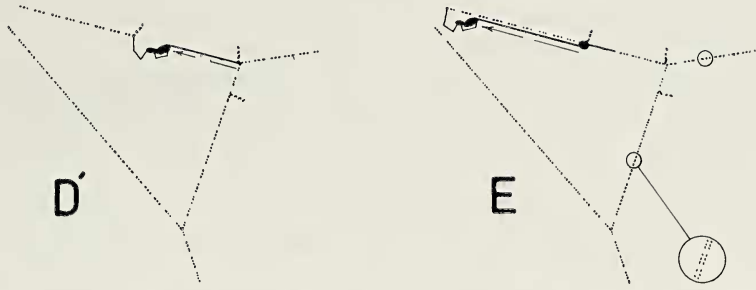
Figure 7.—Sequence of final events in *P. vicina* frame construction Type D (stages A-C as in Fig. 6) (conventions as in Figs. 3 and 4).

The impending approach of PHR was signalled when the spider modified radii (partially or completely replaced them or added frame lines) one after another in strict sequence moving around the web. An example of such a sequence was a spider which began this stage with radii at 1, 2, 3, 5, 6, 7, 9 and 10:00 positions.. First it modified the 9:00 radius, then, in order, those at 7, 6, 5, 3, 2, 1, and 10:00. In 30 webs in which positions of modified radii were noted, the last five modifications on radii preceding PHR were all on adjacent radii and all progressed in a consistent direction except for two cases in which the spider skipped a single radius.

In addition, when the direction in which a frame line was laid was noted ($N = 50$), the frame was always laid so that the exit radius was on the "leading" or far
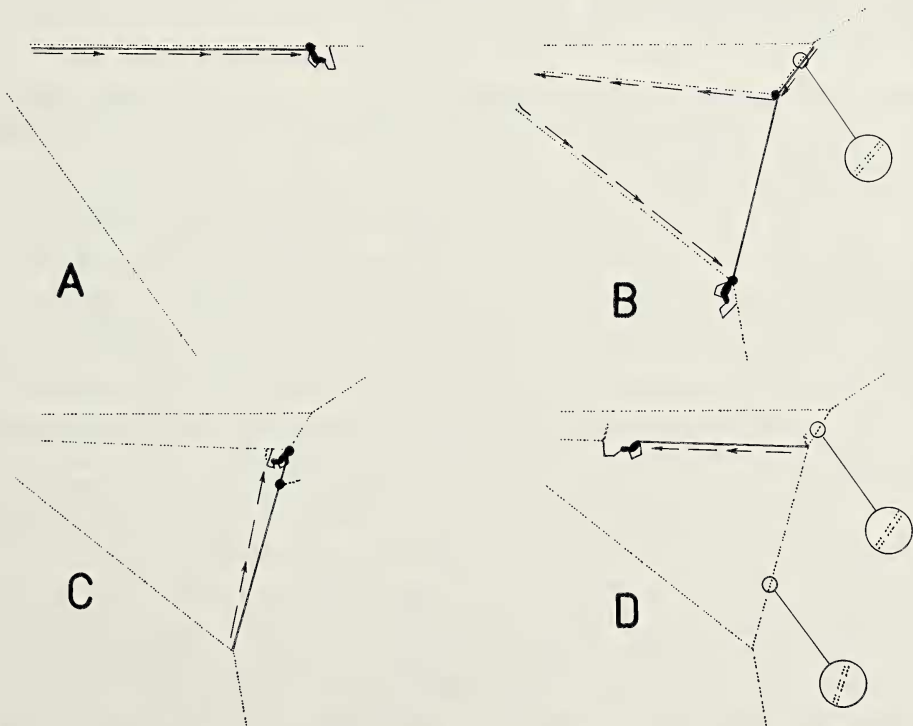

Figure 8.—Sequence of events in *P. vicina* frame construction Type E (conventions as in Figs. 3 and 4).
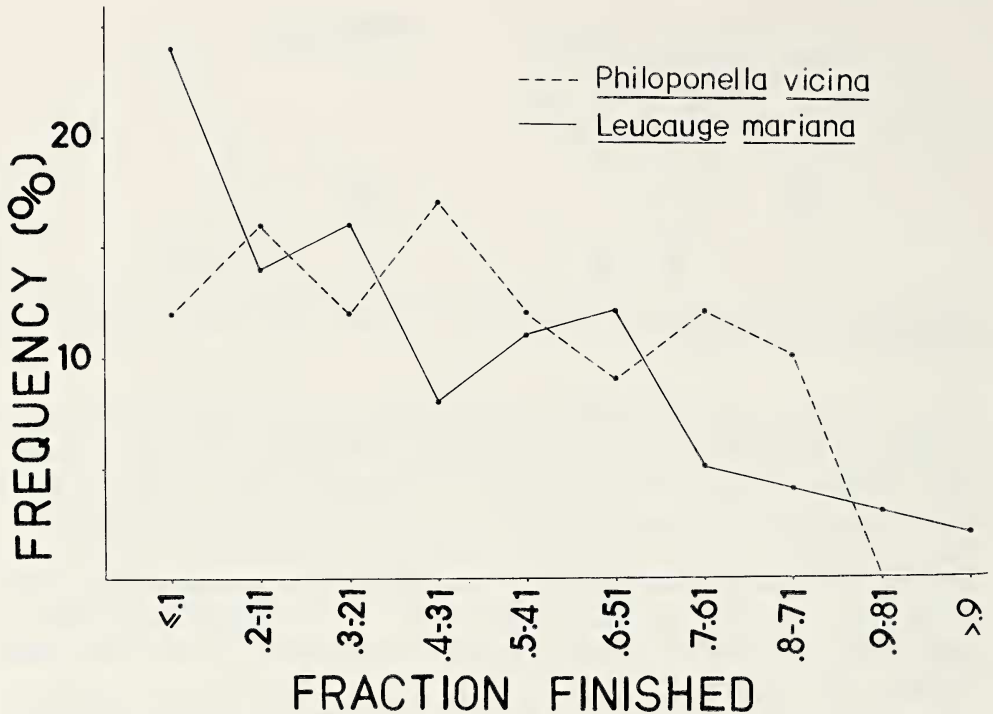
Figure 9.—Relative numbers of frame lines built at different stages of orb consturction by *P. vicina* (dotted line) (*N* = 58 frames in 17 orbs) and *L. mariana* (solid line) (*N* = 92 frames in 18 webs) (stage of construction indicated by fraction of final number of radii already present). Since some observations began after the first few radii had been laid (inset in Fig. 15), the frames laid in the very earliest stages (< 0.20) are under-represented.

side of the sector that would be spanned. Thus in the web just mentioned, the exit on the 9:00 radius resulted in a frame connecting 9 to 10, that on 7 resulted in a frame from 7 to 9, etc.

The last behaviors preceeding PHR tended to result in smaller modifications of the web. The last modification before PHR was more likely to be a partial replacement than a frame construction or radius shift (*P* < 0.01 comparing last modification before PHR with preceeding five in 27 webs). In addition, the partial replacements performed during one or two radial modifications just preceding PHR (*N* = 24 in study webs) more often involved only the inner 20% portion of the radius' length than those performed earlier (*N* = 54) (*P* < 0.01).

III. Proto-hub removal (PHR): The spider simultaneously cut the accumulation of loose silk free from where the radii converged, ingested it, and reattached the radii. In some, but not all cases, the new line joining the radii was nearly circular (Fig. 2). In 13 webs which had an average of 17.7 ± 4.4 radii when finished, an average of 7.3 ± 2.1 radii were present when the proto-hub was removed.

IV. After PHR: Following PHR, the spider added new radial lines as well as occasional frames (Fig. 9). Usually the spider chose to exit along the leading edge of a sector (100 of 127 in 31 webs) as in frame construction preceding PHR, but in other respects the behavior was quite different. Existing radii were seldom replaced following PHR (7 of 176 trips from away from the hub in the study webs). Hub spiral construction after each trip away from the hub began abruptly, usually and perhaps always starting with the first radius after PHR (occasionally

it was difficult to be sure of this point for the first new radius or two). All new radii were added without breaking lines, as described in Eberhard 1972 and 1982 (character F3), and radial lines were continuous with the hub spiral. Frame construction differed from that preceeding PHR; it did not involve breaking previous lines on the way out from the hub, and it included sealing the break in the new radius part way back to the hub (types D and E—see Figs. 7 and 8).

Leucauge mariana.—Nothing corresponding to PHR was ever performed by *L. mariana* in the early stages of construction. Unless otherwise noted, all data are from the study webs.

I. Exploration: As with *P. vicina* (and *Araneus diadematus*—Reed 1968), preliminary placement and removal of lines prior to construction proper was generally carried out intermittently over several hours. The same behaviors were used, including breaking and reeling while replacing lines, shifting attachment points of lines, descent on single lines (often reaching obects below the web without making an attachment), and production of airborne spanning lines. The only exploratory *P. vicina* behavior not performed by *L. mariana* was wrapping of accumulated loose silk from the previous web; this difference was not surprising since the very extensible wet sticky silk of *L. mariana* contracted immediately into relatively compact masses on its own when web lines were cut. *L. mariana* often made long airborne spanning lines, and was much more likely to move far from the previous website than was *P. vicina*. When on lines near the wire hoop, spiders sometimes bounced up and down as they moved, a behavior not seen in other situations or in the other species. Possibly this movement serves to test the rigidity of the substrate.

II. Frame and radius construction: Eventually the spider's activities became concentrated around a central point where three or more lines intersected (the web's future hub) and the spider repeatedly moved toward the edge and then returned to this point. Some radii were partially replaced, and new radii as well as frame lines were laid. Partial radius replacement was like that of *P. vicina*, and new radius construction was as described by Eberhard 1982 (character F1). Frame construction varied (types A-D in figs. 10-13), but never included breaking the new frame and shifting the attachment outward as in *P. vicina* (e.g., Fig. 4C). Instead, the spider usually made a dragline attachment to the new frame, and then a second attachment to the frame just on the far side of the new radius as it swung its abdomen in this direction prior to returning to the hub (Fig. 14) (a similar slight separation of the second attachment in the same direction occurs in *Metazygia* sp., *Micrathena* sp., and *Eriophora* sp.—Eberhard unpub.). The older frame segment (dotted lines between attachment points [large dots] in Fig. 14) often sagged perceptibly when the spider broke the radius and returned to the hub. Occasionally a spider reinforced or perhaps tightened a frame line by adding a line attached on either side of the new radius before returning to the hub.

Spiders never modified three or more adjacent radii in orderly sequences, nor were frames ever built in strict order in adjacent sectors as in *P. vicina*. Usually it was not possible to observe if the spider made more than a single attachment at the hub after laying a radius, but recognizable hub spiral was almost never laid until radii were complete. One otherwise apparently normal spider seemed to have difficulty in making attachments, and paused perceptibly each time it attached; this spider made only a single attachment as it arrived at the hub after laying most radii; occasionally it made up to three attachments prior to leaving to build the next radius.
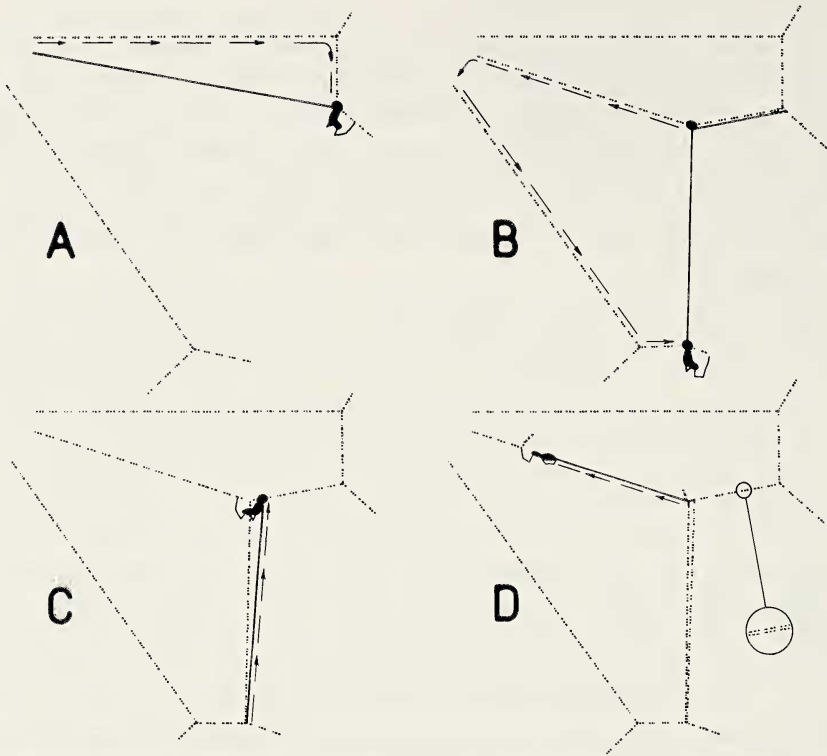
Figure 10.—Sequence of events in *L. mariana* frame construction Type A (conventions as in Figs. 3 and 4).
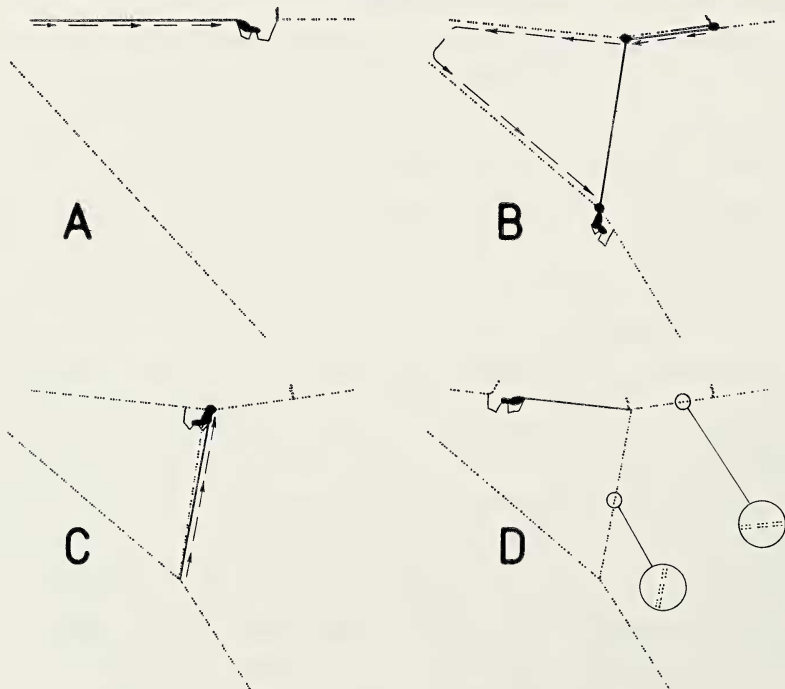

Figure 11.—Sequence of events in *L. mariana* frame construction Type B (conventions as in Figs. 3 and 4).
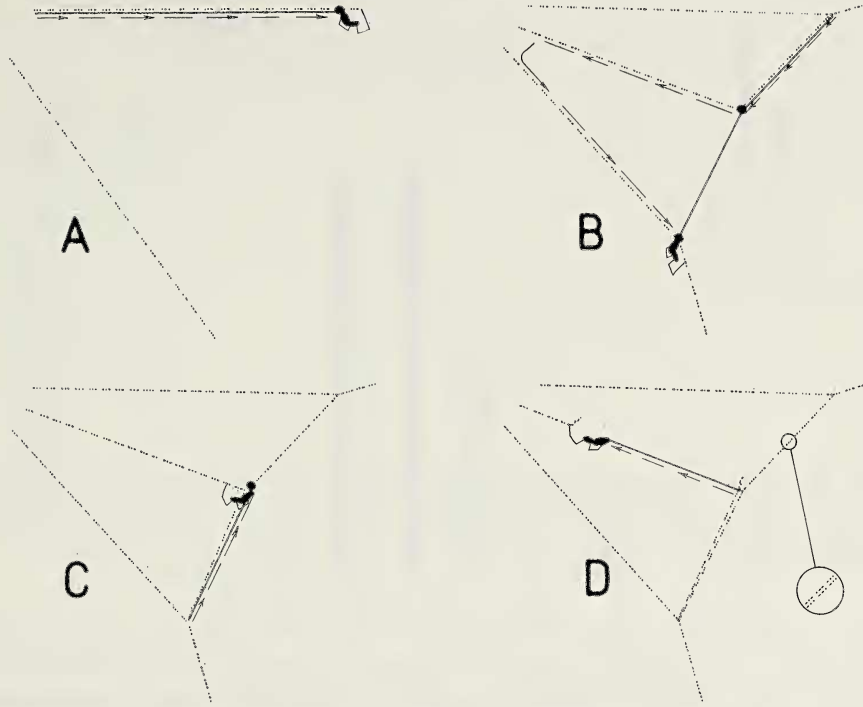
Figure 12.—Sequence of events in *L. mariana* frame construction Type C (conventions as in Figs. 3 and 4).
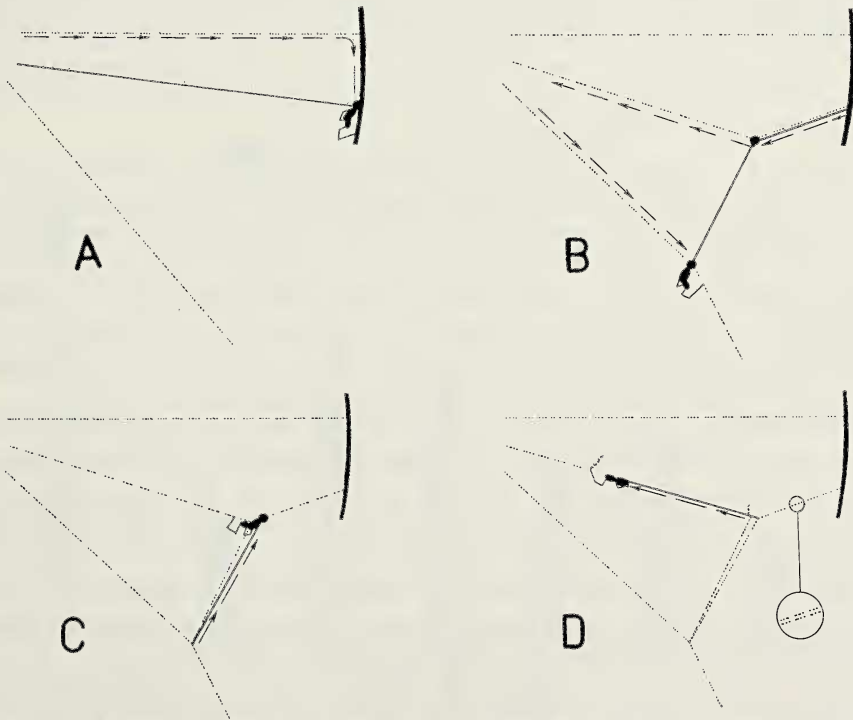

Figure 13.—Sequence of events in *L. mariana* frame construction Type D (conventions as in Figs. 3 and 4).
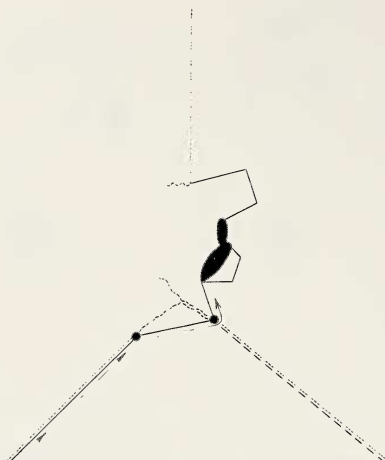
Figure 14.—Details of last attachment in frame construction sequences of *L. mariana* (e.g., D in Figs. 12, 13). As the spider breaks the radius (vertical line) it attaches to the frame on both sides of the original radius-frame attachment, thus allowing a short segment of the frame to go slack (conventions as in Fig. 3).

Frame construction was intercalated with other activities such as radius construction, and showed a similar distribution throughout web construction to that in *P. vicina* (Fig. 9). Partial replacements of radial lines had the same general pattern (Fig. 15), but had a stronger tendency to occur later in construction ($P <$ 0.05) comparing webs >30% finished with earlier stages of construction in the two species). Frames were less likely to be built in succession by *L. mariana* than by *P. vicina*: the behavior immediately preceding frame construction was more often radius construction, and less often frame construction in *L. mariana* ($P <$ 0.01 for both, $N = 84$ for *L. mariana*, 68 for *P. vicina*). The most common major type of frame construction (Figs. 10-13) was A (60% of 93 in study webs), followed by C (19%), B (15%), and D(5%).

In contrast to *P. vicina*, the choice of exit radius was not consistent. In only 100 of 211 cases was the side chosen the same as that for the previous radius ($P > 0.5$). The angles between the last six radii were also larger in *L. mariana* (Fig. 16, $P < 0.01$). This was due to the tendency of *L. mariana* to lay successive radii in opposite halves of the web rather than to there being fewer radii in *L. mariana* webs; finished *L. mariana* webs averaged 21.4 ± 3.2 radii while those of *P. vicina* averaged 18.3 ± 4.1. Nearly 60% of the radii in *L. mariana* webs made angles of more than 120° with the radii that immediately preceeded them.

Nephila clavipes.—Mesh on either side of the orb was built prior to and during the first stages of orb construction. No behavior resembling PHR was observed. The mesh was also frequently extended after part of the sticky spiral was complete. Mesh construction was very complex, but included some components of radius and frame construction. It will not be described here.

I. Exploration: Exploration behavior included descents on single vertical lines, occasional long periods of immobility, and "around the corner" substrate attachments. On four occasions a spider went all the way (360°) around a wire or a string in making such an attachment. A central area (the future hub) where lines converged was always established very early in construction, both in webs built from scratch and those with a mesh already present. Commonly the spider
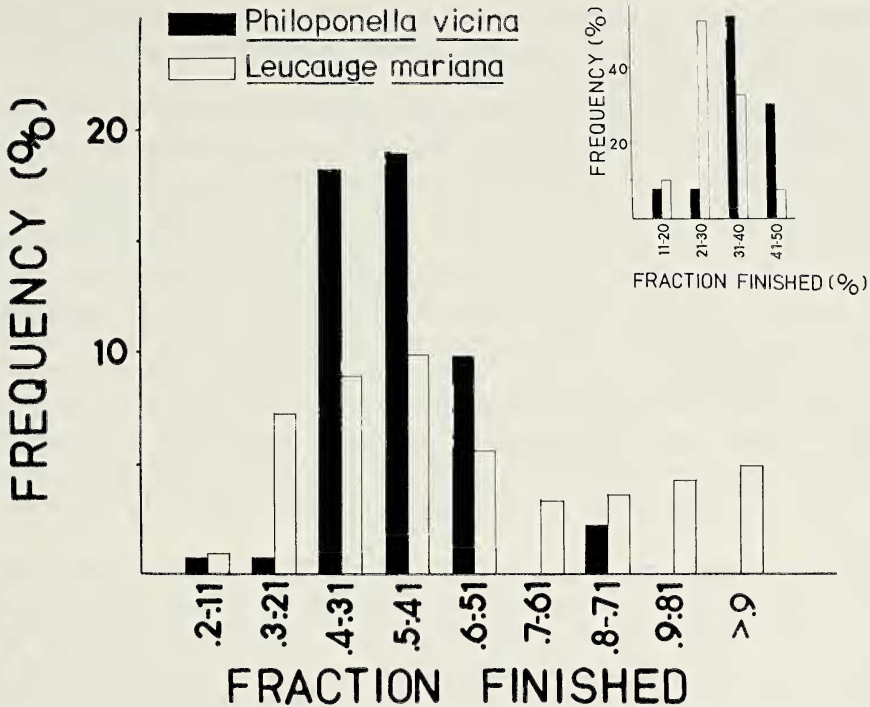
Figure 15.—Relative numbers of partial replacements at different stages of orb construction by *P. vicina* ($N = 72$ replacements in 17 webs) and *L. mariana* ($N = 154$ replacements in 40 orbs) (state of construction indicated by fraction of final number of radii already built). Since some observations began after the first radii had been laid, replacements made in the very earliest stages (<0.20) are under-represented (inset shows the percentage of the final number of radii already present when observations began).
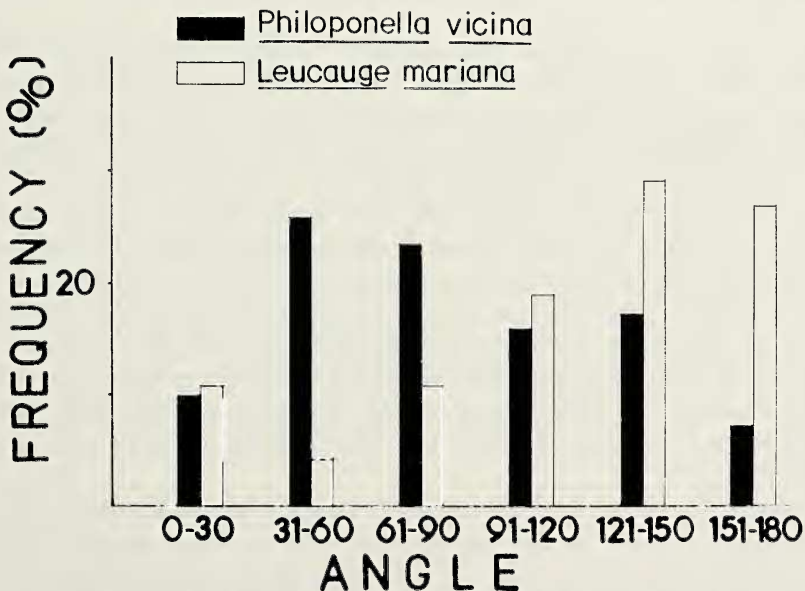
Figure 16.—Distributions of angles between successive radii for the last five radii laid in 16 *P. vicina* and 18 *L. mariana* webs (partial replacements are not included).

expanded the web by walking to the edge and then moving sideways along the substrate before attaching its dragline. Spiders usually slowed appreciably as they moved from a silk line onto the substrate.

Although spiders usually returned from excursions away from the hub along the dragline they had laid on the way out, they never performed one of the most common behaviors of *P. vicina* and *L. mariana*: move away from the hub, attach the dragline, then turn back and break and replace the dragline just laid while moving back to the hub (e.g., Fig. 3). Spiders were capable of breaking and reeling the line they were on, but did this only while removing lines which had not just been laid, and nearly always (40 of 42 times) while moving away from the hub. Many other lines were broken and then simply released and allowed to sag free; breaks of this sort often occured while the spider was at the hub (14 of 43 cases). Since lines were seldom shifted or replaced, the site of the hub did not change as lines were reconnected as sometimes occurred in *P. vicina* and *L. mariana*. In one case, however, a second hub developed during mesh construction and became the hub of the orb while the first "hub" came to be in the mesh on one side.

Some radii were added early in orb construction without breaking lines: the spider moved away from the hub on a pre-existing radius and then sideways along a frame line or the substrate, attaching its dragline and returning along it, reinforcing it with a second dragline. Other excursions of this sort (6 of 14) resulted in two new radial lines, as the spider continued sideways after the first attachment and attached its dragline a second time before returning to the hub along the line laid on the way out. Neither of the other two species exhibited these behaviors.

II. Frame and radius construction: Frames were never laid in strict order as in *P. vicina*. Hub loop construction did not begin until several radii, a substantial amount of mesh, and often some of the frames had been laid. Once it commenced, hub loop construction occurred after each excursion to build radii or frames.

Frame construction behavior was extremely variable. Types A and B (Figs. 17, 18) were most common (frequencies were 39 and 12% respectively in 101 sequences observed). Twenty-eight additional types of frame construction were seen, none repeated more than three times. Some alternative behaviors were closely related to the most common types. For example one (Fig. 19) was the same as B except for an extra trip across the sector. The points where attachments were made in both A and B varied substantially. Thus the variant in Fig. 20 involved the attachment of a second new radius to the end of the first, and that in Fig. 21 attaching the second new radius beyond the first as the spider moved along the frame; both of these behaviors were similar to Type A. Other variants involved laying similar lines but using alternative paths to lay them (Fig. 22), and breaking and reeling lines instead of simply walking along them (Fig. 23). Still further variants, however, had little relation to more typical patterns (Figs. 24, 25).

All types of frame construction involved laying two radial lines in the process of constructing a single frame, and none involved breaking any of the lines laid while the frame was being made; in both respects *N. clavipes* behavior differed from all types of frame construction seen in *P. vicina* and *L. mariana*.
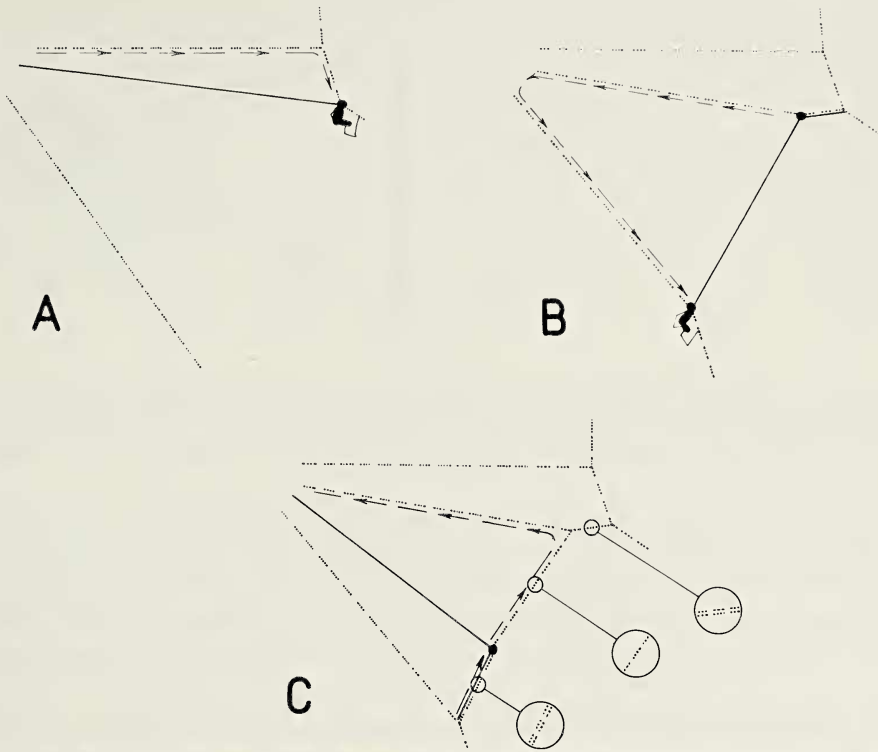
Figure 17.—Sequence of events in *N. clavipes* frame construction Type A (conventions as in Figs. 3 and 4).
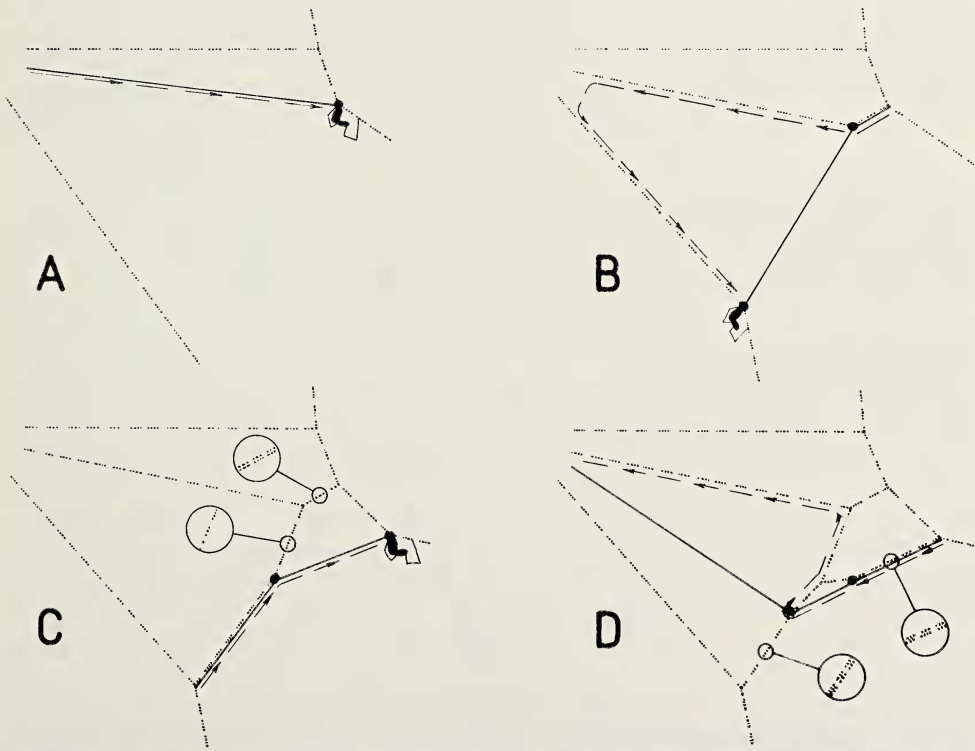

Figure 18.—Sequence ot events in *N. clavipes* frame construction Type B (conventions as in Figs. 3 and 4).
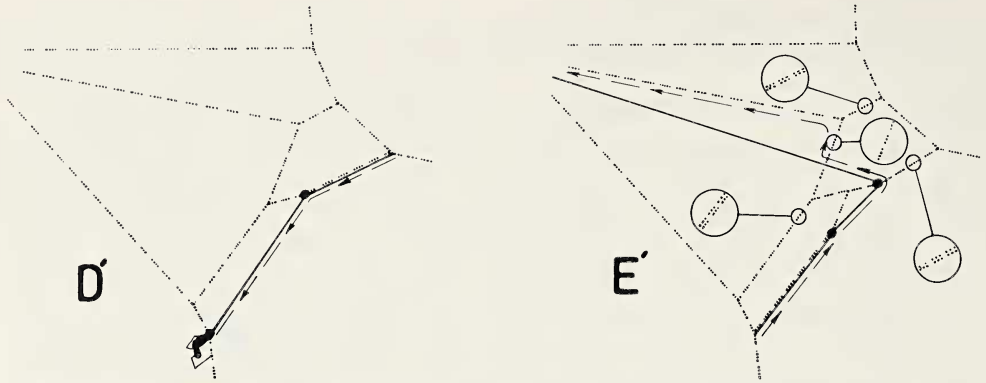
Figure 19.—Sequence of late events in *N. clavipes* frame construction. Behavior was similar to that in Fig. 18 (stages A-C were identical) except the spider made a trip a cross the entire sector (D′) before crossing to lay the second radius and return to the hub (E′) (conventions as in Figs. 3 and 4).

Radius construction usually also involved two attachments to the frame and resulted in two radii being laid during each trip away from the hub (Eberhard 1982, character F2). In 44 of 353 cases, however, I was certain that only a single attachment was made at the frame, and the second dragline was laid alongside the first (Eberhard 1982, character F3). Nearly all of these exceptional single radii were relatively short, and 34 of 44 were above rather than below the hub ($P <$ 0.001 compared with double radii). The spider always left the hub on the
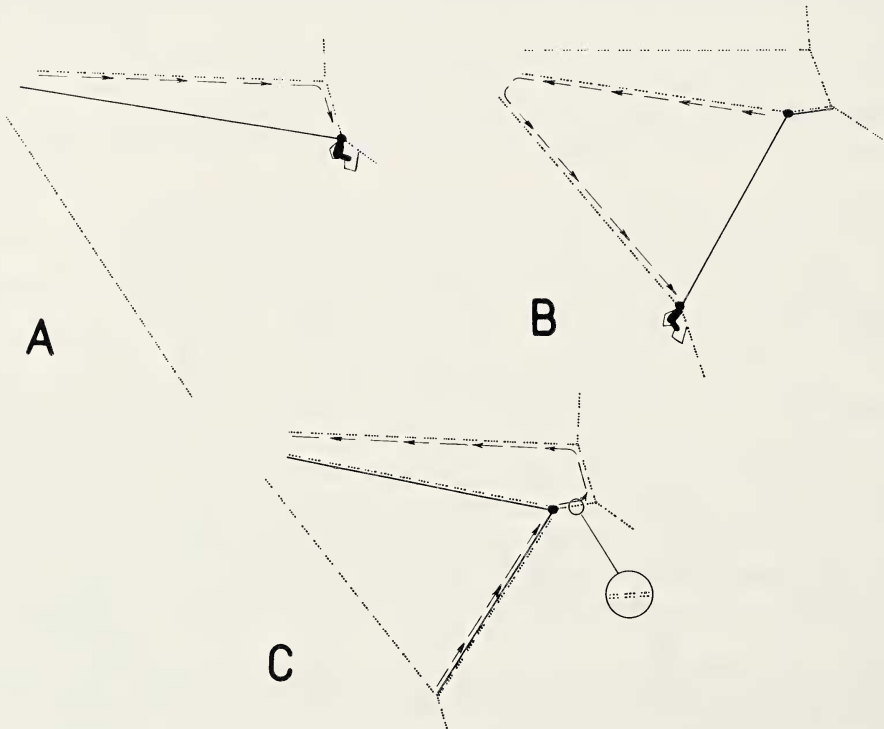

Figure 20.—Sequence of events in *N. clavipes* frame construction similar to that in Fig. 17 except the spider attached the second radius right at the point on the frame where the first was attached (C) (conventions as in Figs. 3 and 4).
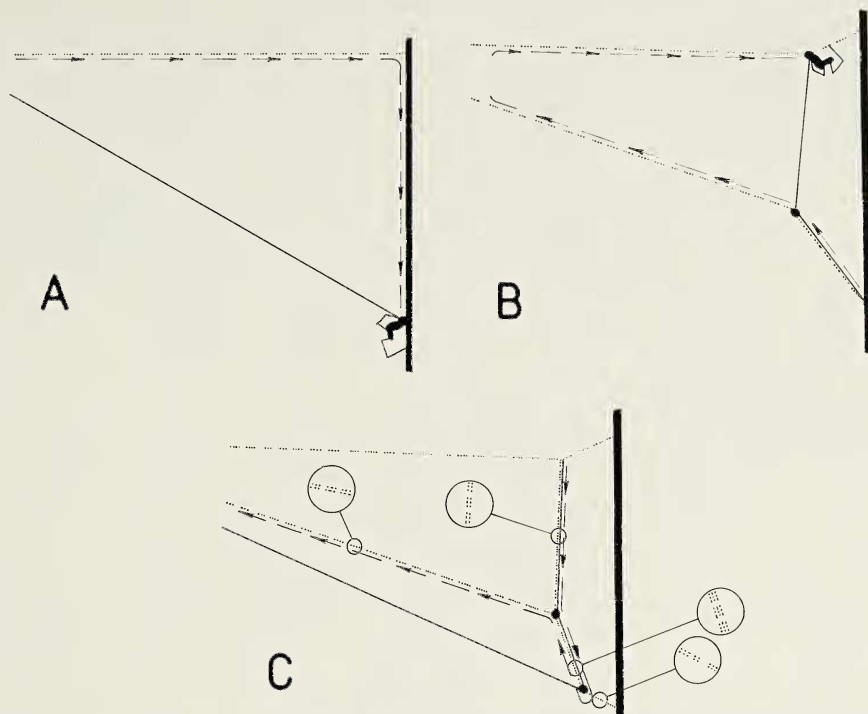
Figure 21.—Sequence of events in *N. clavipes* frame construction similar to that in Fig. 17 except the spider moved along the new frame past the site of the first new radius before attaching the second new radius (C) (conventions as in Figs. 3 and 4).

uppermost of the two radii bounding the sector where the radial lines would be laid ($N > 200$). In four cases a spider interrupted hub loop construction and started away from the hub as if to lay radii, but turned back after moving only a mm or so and resumed hub construction. Similar "false starts" occur in *U. diversus* (Eberhard 1972).

Spiders showed individually consistent differences in the pattern of velocities of movement during radius construction. Some moved inward and outward at more or less the same, relatively slow rate. Others moved part way out relatively slowly, then moved very quickly the rest of the way out, along the frame, and part way in, then slowed again as they approached the hub.

As first described by Hingston (1922) and Wiehle (1931), radius construction continued after the spider widened the space between the loops it was making at the hub, thus changing from hub to temporary spiral construction. Most radii laid during temporary spiral construction were below rather than above the hub (103 of 115 compared with 91 of 238 radii laid earlier, $P < 0.001$).

Other uloborids.—*Hyptiotes cavatus* (Hentz) build triangular webs that probably represent segments of orbs. Previous accounts of construction behavior (Nielsen 1932; Marples and Marples 1937; Eberhard 1982) are not entirely clear on the early stages of construction. I observed only a single web of *H. cavatus* being built, but was able to understand some of what I saw. There was no behavior corresponding to PHR. The single frame was built after two radii were in place, and resembled type B pre-PHR behavior in *P. vicina* in both the replacement of the exit radius and the shift of the frame attachment outward
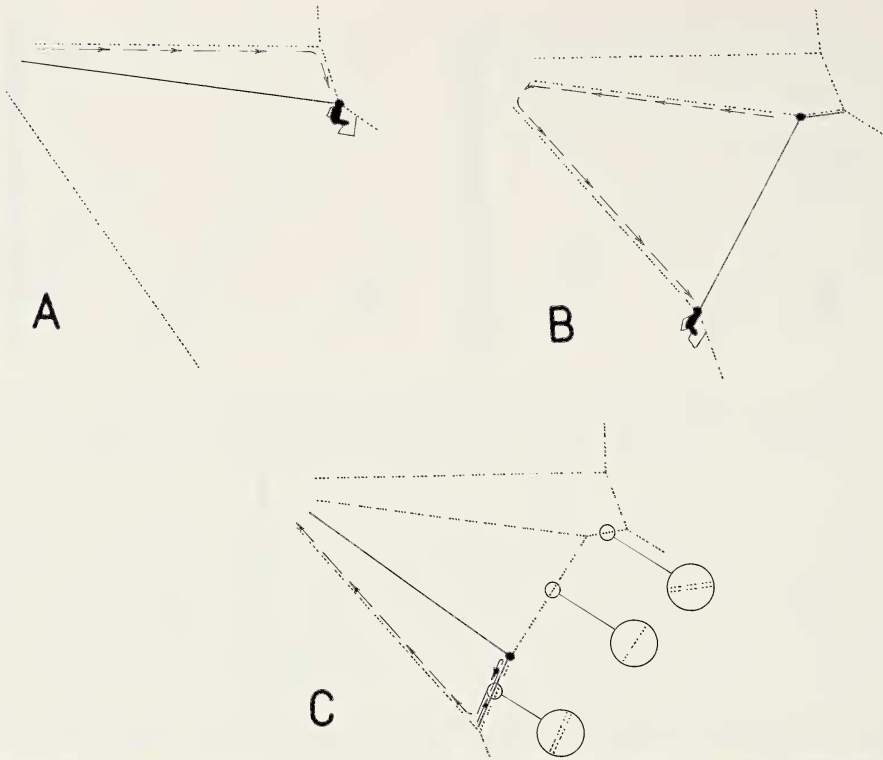
Figure 22.—Sequence of events in *N. clavipes* frame construction similar to that in Fig. 17 except the spider turned back after attaching the second new radius (C), using the second of the two exit radii to make its final return to the hub (conventions as in Figs. 3 and 4).

(Fig. 5). It bore no resemblance to the frame construction behavior reported by Marples and Marples (1937) for *H. paradoxus*. The other two radii were then added without any lines being broken, and without any attachments other than the initial attachments at the hub and the frame. Temporary spiral construction began immediately after the fourth radius was laid, without any hub spiral having been laid. Thus *H. cavatus* radius and frame construction resemble pre-PHR behavior in *P. vincina* except for the last two radii; these resembled post PHR construction except that no hub was made. The descriptions of *H. paradoxus* construction by Marples and Marples (1937) agree on all of these points other than the exception noted above.

Though observations on other genera are still needed, additional observations of construction of single webs by *P. tingena, Uloborus trilineatus*, and *Zosis geniculatus* suggest that several of the special behaviors seen in *P. vicina* and *U. diversus* are widespread in uloborids. All species replaced a proto-hub early in radius construction, and broke newly laid frames to shift the frame attachment outward during frame construction (e.g., Fig. 4C). Only after PHR did *U. trilineatus* and *Z. geniculatus* make series of hub attachments during radius construction. Both *P. tingena* and *U. trilineatus* modified a series of radii just before PHR; in *U. trilineatus* I noted that these radii were in strict sequence as in *P. vicina*.

Other araneoid orb-weavers.—Prior to beginning this study, I observed frame construction in 19 tetragnathid and araneid genera (*Nephilengys, Tetragnatha,*
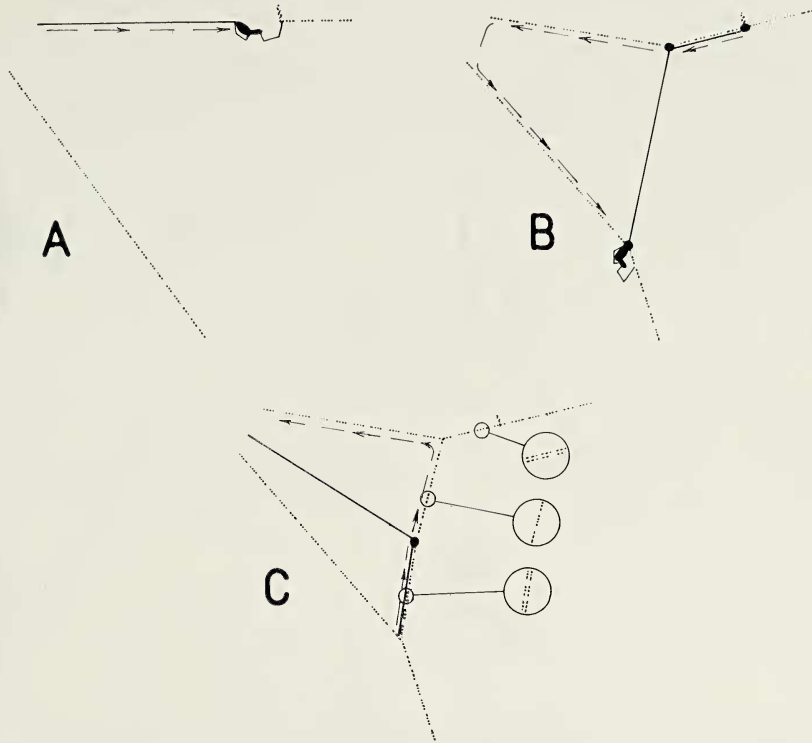
Figure 23.—Sequence of events in *N. clavipes* frame construction similar to that in Fig. 17 except the previous radius on which the spider moved away from the hub was broken and replaced (A) (conventions as in Figs. 3 and 4).

Chrysometa, Gasteracantha, Micrathena, Pronous, Alpaida, Argiope, Cyclosa, Cyrtognatha, Enacrosoma, Eriophora, Eustala, Hypopthalma, Larinia, Metazygia, Parawixia, Neoscona, Verrucosa, Wagneriana, and *Witica*), in the theridiosomatid *Epeirotypus* sp., and in the mysmenid *Mysmena* sp. While some of my notes do not mention how early in web construction my observations began, very early stages were certainly observed in *Nephilengys, Gasteracantha, Micrathena* (three species), *Alpaida, Cyclosa, Hypophthalma, Metazygia, Neoscona, Tetragnatha, Epeirotypus,* and *Mysmena*. In no case did any species perform any behavior similar to PHR; since I had observed PHR in *U. diversus* before I made these observations, I am confident that I would have noted anything similar to PHR if it had occurred.

At the conclusion of the study I observed the construction of webs by a different *Metazygia* sp. and *Acacesia hamata*, and again failed to note any behavior remotely similar to PHR.

DISCUSSION

A. Distinguishing characters and their homologies.—In order to compare the behaviors of different groups, it is necessary to first decide which behaviors differ, and which differences or similarities are homologous. Unfortunately, these descriminations are influenced by what seem to be unavoidably subjective decisions. Analysis at a fine level (e.g., movements of given legs) can give
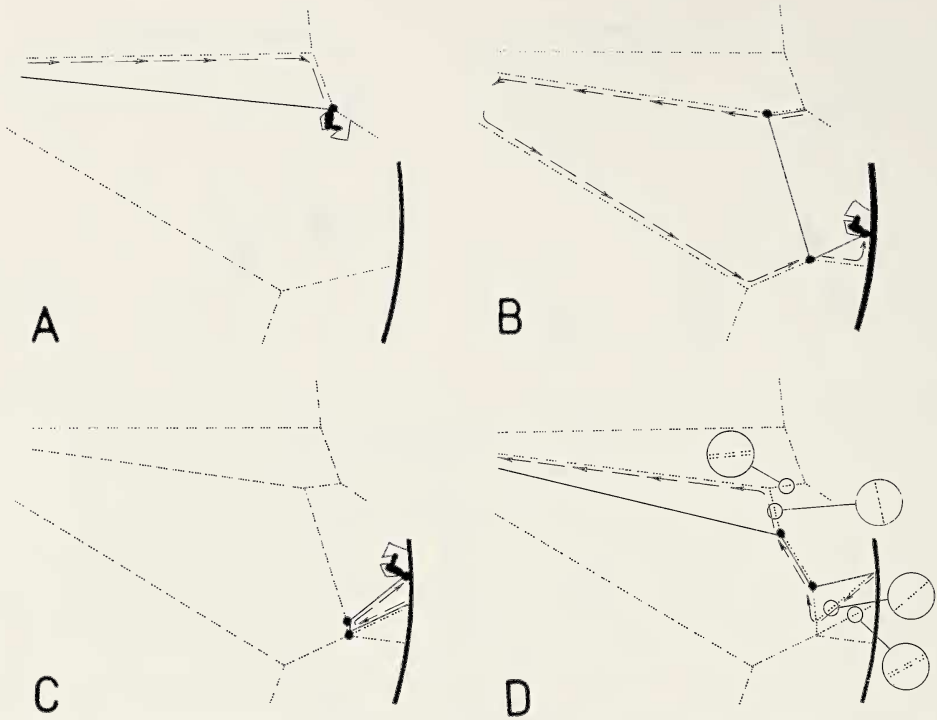
Figure 24.—Sequence of events in complex *N. clavipes* frame construction behavior (conventions as ijn Figs. 3 and 4).

different results from that at higher levels of organization (e.g., inclusion of the context in which the movement is performed). For instance, I have previously interpreted the tapping behavior of legs I to the side during sticky spiral construction to locate previously laid lines as a possible synapomorphy of Araneidae (Eberhard 1982). But undoubtedly many other orbweavers, and indeed other spiders which do not make orbs occasionally tap their front legs laterally to locate lines (or other objects). So if tapping to the side is itself the unit being compared, the behavior is not a synapomorphy.

The problem of context is acute in behavior since a common and important pattern in behavioral evolution is that of changes in context; a given movement or sequence of movements is transposed from one context to another. This pattern of evolution implies that the standard cladistic techniques of weighting characters equally is inappropriate, since (all other things being equal) convergence via such transpositions is more likely to evolve than is convergence via independent invention or reinvention; transpositions should thus be given less weight in constructing phylogenies.

How great must a change in context be for a homology to be rejected? How can the "size" of a change in context even be measured? These questions seem not to have straight-forward answers. In the example of tapping behavior it seems relatively clear that including the context of the leg movement as a part of the character is reasonable. In other cases, however, this decision is more difficult. Take for example the proto-hub removal behavior of uloborids described in this study. Many araneoid spiders remove the central area of their hubs near the end of orb construction (e.g., Eberhard 1982, 1987c; Coddington 1986a). Is this
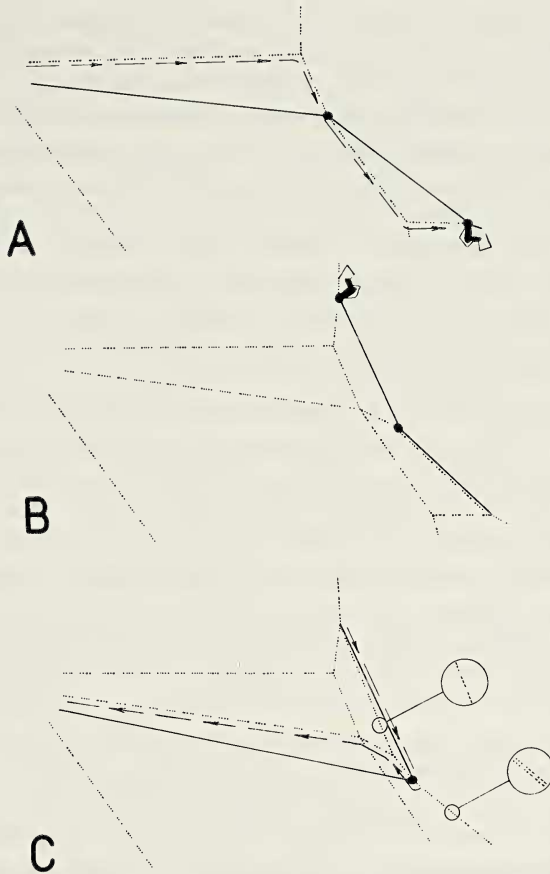
Figure 25.—Sequence of events in complex *N. clavipes* frame construction behavior (conventions as in Figs. 3 and 4).

removal behavior homologous with the PHR of uloborids, but simply displaced to a later position in the sequence of construction? Or is it an independently derived process which has converged on PHR in general form?

Similar problems occur in simple descriptions. Is the behavior in Fig. 11A-B, where *L. mariana* stopped and attached to a line before reaching the substrate different from that in Fig. 13B, where the spider moved past the end of a silk line and laterally (the only direction possible on the wire hoop) before attaching? These problems are related to a general problem plaguing taxonomy—that of deciding how to code characters (behavioral or otherwise), and of the lack of information correlating the amount of phenotypic difference with the degree of improbability that a given phenotype could be derived independently.

As I have no certain answers to these types of questions, the practice adopted in both the descriptions above and the discussion below is conservative: claims of homology are minimized, and differences are thus emphasized. This focus stems both from a reaction against previous oversimplified accounts of construction behavior, and from one of the basic objectives of this study: to provide additional characters to help in the resolution of the controversy surrounding the phylogeny of orb weavers (the final answer to which obviously must depend on as many characters, behavioral and otherwise, as possible). Future workers may decide,

one would hope with better criteria and/or evidence than those which are presently available, that some distinctions made here are unjustified, and combine categories. The opposite process, splitting two categories from a single one in which differences had not been reported, would not be possible.

B. Comparisons between species.—One consistent difference between frame construction by *P. vicina* and that of the araneids *L. mariana* and *N. clavipes* was that all frame lines constructed by the uloborid were broken as the spider returned to the first radius laid, and were then shifted outward along this radius (Figs. 4-8). This behavior never occurred in *L. mariana* or *N. clavipes*. These observations agree with Coddington's (1986a) observations of one genus of uloborid and 17 genera of orb-weaving araneoids, and reinforce his idea that this difference may distinguish uloborids and araneoids.

A second difference was that *P. vicina* usually chose exit radii that were on the leading edges of sectors to be filled during both frame and radius construction, while *L. mariana* showed no preference. The same preference was shown by *U. trilineatus* and by *U. diversus* (at least during frame construction—Eberhard 1972). The difference with *L. mariana* may be partly related to the fact that the uloborids make hub spiral between all or nearly all radii laid after PHR, and are thus turning in an orderly manner at the hub, while *L. mariana* generally makes no hub spiral until all radii are in place. In non-horizontal webs, both *L. mariana* (Eberhard unpub.) and *N. clavipes* generally exit on the upper of the two radii bounding the sector where the radius or frame is to be laid, just as usually occurs in araneids such as *A. diadematus* Cl. (Reed 1968), *Micrathena plana* (Koch), *Verrucosa* sp., and *Cyclosa caroli* (Hentz) (Eberhard unpub.).

The most dramatic differences between the behavior of *P. vicina* and the araneoids are associated with PHR. PHR always occurred in undisturbed *P. vicina*, but never occurred in *L. mariana* or *N. clavipes*. In addition, PHR in *P. vicina* was always preceded by a strictly ordered sequence of frame construction and radial modifications on adjacent radii, while the order of operations in the early stages of *L. mariana* and *N. clavipes* webs did not follow strict sequences involving adjacent radii. Examination of literature accounts of uloborid and araneoid behavior plus the brief observations of other uloborids and araneoids reported here suggest that both PHR and strict ordering of frames probably distinguish uloborids from araneoids. No araneoid has ever been reported to perform any behavior during the early stages of orb construction that might correpond to PHR (see detailed observations of Hingston 1922; Tilquin 1942; Koenig 1951; Mayer 1952; Witt et al. 1968 as well as the observations reported here). The most similar behavior is the possibly non-homologous hub replacement (see above) performed by some theridiosomatids and anapids after the web is otherwise complete (Eberhard 1982, 1987c; Coddington 1986a). On the other hand, all species of orb weaving uloborids that have been observed (two *Uloborus*, two *Philoponella*, and one *Zosis*) show clear PHR.

The few accounts of sequences of frame lines in araneids (Tilquin 1942 on *Araneus* sp. and *Argiope*; Mayer 1952 on *Araneus diadematus*; Dugdale 1969 on *Micrathena gracilis*), do not show a strict sequence of frames in adjacent sectors of the orb, and Tilquin (1942) states that sequences of frames vary and that radius construction often interrupts frame construction (p. 208 ff.). The only two uloborid orb weavers carefully checked in this study, *U. trilineatus* and *P. vicina*, both modify adjacent radii in strict order immediately preceeding PHR, often

making a series of adjacent frame lines. *U. diversus* also often makes series of adjacent frames (Eberhard 1972). Thus, as far as these incomplete data go, orderliness in frame construction also distinguishes uloborids from araneoids.

Angles between successive radii were larger in *L. mariana* than in *P. vicina* and the same difference apparently occurs when the araneid *M. gracilis* is compared with the uloborid *U. diversus* (Eberhard 1972). Apparently araneids often tend to lay successive radii on nearly opposite sides of the web (Hingston 1920; Witt et al. 1968; Uetz 1986). This difference is probably related to the fact that uloborids lay hub spiral during radius construction while most araneoids lay less or none. Radii on opposite sides may be advantageous in balancing tensions at the hub, but such adjustments would probably not be practical for a spider which is also laying hub spiral, since an excessive number of hub loops would be necessary to allow completion of radius construction, especially in view of the relatively high numbers of radii in some uloborid orbs (Eberhard 1986).

Another possible difference was that *P. vicina* used legs IV to reel in slack silk during frame construction while the others did not. Both *L. mariana* and *N. clavipes* tightened slack frame lines using a different behavior involving the front rather than rear legs. (*L. mariana* was never seen to reel in any line with a leg IV in any context, but *Nephila* sometimes ascends its dragline backwards after attacking prey—Robinson and Robinson 1973). Other uloborids (*Hyptiotes*—Marples and Marples 1937, and Opell 1985; *Miagrammopes*—Lubin et al. 1978) reel in lines with legs IV.

Observations of a slow-moving *L. mariana* as it laid radii revealed that the spider usually failed to lay hub lines between successive radii. Hub lines were also not laid during the early stages of radius construction by *N. clavipes*. These observations are not in accord with Coddington's statement (1986a: 344) that both "araneoids and uloborids construct frames and radii as a subroutine within hub construction." Since it is often very difficult to determine how many hub attachments are made between successive radii (I was generally unable to decide, for example, whether multiple attachments were made by *P. vicina* before PHR), Coddington's claim should be treated with caution.

Changes in the types of radius and frame construction behavior before and after PHR which are similar to those of *P. vicina* appear to occur in *U. trilineatus*, *Z. geniculatus*, and *P. tingena*. Similar changes in frame (but not radius) construction occurred as web construction in *L. mariana* progressed. In all cases there was a gradual reduction in the removal of lines already in place in the web.

The order and kinds of lines laid during frame construction behavior was clearly variable in each of the three species studied in detail here. Both *P. vicina* and *L. mariana* had several common patterns, and additional rare variations. Probably a few further variants remain to be described, perhaps including some of the sequences I saw but failed to understand (see Methods). The behavior of *N. clavipes* was much more variable, and the total number of variations may be quite high (>50?). Some literature descriptions of other species' behavior may represent still further variations (see Tilquin 1942 and Reed 1968 on *Araneus*; Marples and Marples 1937 on *Hyptiotes*). This variability contrasts with the stereotypy seen in later stages of orb construction (Tilquin 1942; Eberhard 1982). As has been noted before (Witt et al. 1968; Eberhard 1972), an orb weaver gradually isolates itself from its surroundings and from the need to respond to

them as it builds, and it is perhaps not surprising that building behavior in later stages is more stereotyped.

Some shifts in *P. vicina* behavior before and after PHR are not entirely consistent, and may represent imprecision in its behavior (Eberhard in press). For example, behavior typical of pre-PHR such as short partial replacements occasionally appeared just after PHR (6 of 130 replacements in the study webs). Such mixing was especially pronounced when spiders built after their first radii and frames of the morning had been destroyed.

C. Implications regarding the evolutionary origin(s) of orbs.—Several lines of evidence from this paper suggest that the transitions in building behavior postulated by the monophyletic and polyphyletic theories of the origin of orb webs differ less than has been previously appreciated. Coddington (1986a) noted that the similarity between uloborid and araneoid frame construction behavior argues for a monophyletic origin of orbs, since other "perfectly feasible alternatives" exist and are actually described in mistaken accounts in the literature. I agree that these published accounts are probably mistaken, but not that they are so obviously feasible for spiders. There are two kinds of mistakes. In one (Comstock 1940; Levi and Levi 1968; Levi 1978) the spider is described as establishing a frame line by running along the substrate from one anchor to another. This is probably usually physically impossible in nature, where webs are often attached to objects which are too separated for the spider to walk directly between them (e.g., many leaves, twigs), and this behavior did not occur even in the wire frames of this study. The other type of error (McCook 1889; Hingston 1920; Dugdale 1969) describes the frames as being laid before any radii are built. But from very early in the exploratory phase of both uloborids and araneoids there are intersections between lines at central points within the area where the orb will be built, and the spider's activities seem organized around these points as it moves out from them toward the edge of the web, then returns (see Tilquin 1942; Koenig 1951; Mayer 1952; LeGuelt 1966; and Eberhard 1972 as well as this study). In fact, this general radial type of pattern of spinning also occurs in other spiders that do not build orbs, and may be very ancient in spiders (Eberhard 1987d). In sum, the possibility that very ancient, pre-orb traits plus "fabricational constraints" (Coddington 1986a) explain the similarity between uloborid and araneoid frame construction rather than more recent common ancestry of the two groups is more likely than suggested by Coddington (1986a).

Two related points deserve mention. Feasible alternatives for radius and frame construction do exist which neither uloborids nor araneoids are known to employ. These involve the spider not retracing the line it has just laid as it returns to the hub (e.g., Fig. 26). Thus the spider's tendency to turn and retrace its steps hubward along the same radial line it has just laid, in preference to using other nearby lines is a character shared by uloborids and orb-weaving araneoids. Whether this character is primitive or derived with respect to that of possible sister groups is not certain. The fact that *Filistata* returns "hubward" (toward its retreat) along the more or less radial line it has just laid while spinning sticky silk (Eberhard 1987d) suggests this may be a primitive trait.

A second point is that the variation in frame construction behavior documented here makes comparisons between uloborids and araneoids more difficult to interpret. For instance, Coddington (1986a) notes that araneoid and uloborid frame construction behavior is "strikingly similar", noting with reference
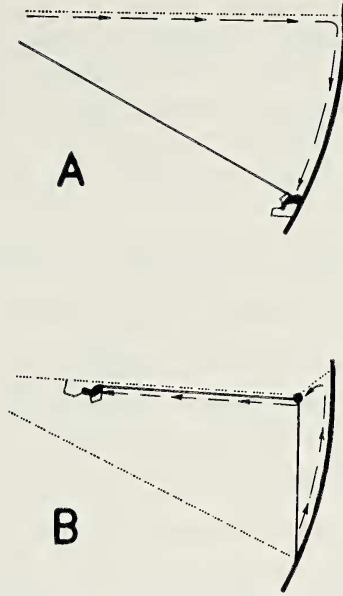
Figure 26.—A simple, feasible frame construction sequence which is apparently never used by orb weavers, in which the spider fails to return to the hub along a newly laid radial line (B).

to *U. diversus* and *A. diadematus* that "both construct a radius each time they construct a frame line." As shown here, this statement is incorrect for both *P. vicina* (Fig. 5) and *L. mariana* (Fig. 11). Some variants of frame construction are similar in the two species (Figs. 4 and 10, 5, and 11, 8 and 12), while others may be unique to one or the other (Figs. 6, 7, 13). It is difficult to decide how great the degree of difference between two behaviors should be to merit recognizing them as being different (see discussion above).

The behavior of *N. clavipes* is probably primitive with respect to that of *P. vicina* and *L. mariana* in at least two respects. The great variability in frame construction is probably primitive, since it seems likely that the evolution of orb construction involved a rigidification, or weeding out of much greater variability in ordering and locations of lines seen in non-orb weavers (Szlep 1965; Robinson and Lubin 1979) (see Eberhard in press). In addition, *N. clavipes* did not break and reel lines during the stages of construction in which deinopids (Coddington 1986b), and uloborids and araneoids do so (this study). This lack of breaking and reeling behavior (which appears to be absent in *Nephilengys* also—unpub.) may also be primitive, since secondary loss would probably be disadvantageous. Breaking and reeling allows the spider to adjust tensions in the web as it is built (Eberhard 1981), to shift the site of the hub as exploration progresses, to eliminate stray lines laid early in the process that are not appropriate for the final web, and to quickly recycle the material from unwanted lines (Peakall 1971; Tillinghast and Townley in press). These functional considerations imply that shifting and replacing lines would be especially important early in orb construction, an interpretation which is supported by the fact that this is when uloborids perform these behaviors.

In addition, the few descriptions of the building behavior of possible outgroups such as theridiids (Szlep 1965; Eberhard unpub. on *Chrosiothes* sp.), pholcids

(Eberhard and Briceño 1985; Briceño 1985) and a diguetid (Eberhard unpub. on *Diguetia canities*) do not include breaking and reeling, suggesting that breaking and reeling may be a derived behavior. The theridiid *Synotaxus* does break and replace dry lines, but the behavior occurs while the spider is producing sticky lines (Eberhard 1977), and may not be homologous with breaking and reeling during frame construction. Clearly, additional data from possible sister groups are badly needed.

If *Nephila*'s highly variable construction behavior and its lack of breaking and reeling in radius and frame construction are both primitive, then the circumstances under which the argument for a monophyletic origin of orbs can be true are limited in such a way that differences between the character state transitions in the mono- and polyphyletic hypotheses are reduced. This conclusion is based on the following considerations. *Nephila* shows several synapomorphies with other orb weaving araneoids (aggregate glands, flagelliform glands, serrate hairs, paracymbium on male palp, inner leg IV pushes sticky silk when attach—Coddington 1986a), and so is likely to be more closely related to these spiders than to uloborids or deinopids. The argument that all orb weavers are descended from a single cribellate orb-weaving ancestor thus has two possible forms with respect to breaking and reeling: either the common ancestor used breaking and reeling behavior and *Nephila* has secondarily lost this ability; or the ancestor lacked this character, and it was acquired independently in both uloborids and other araneoids. Similarly, either the ancestor lacked relatively invariable frame construction, or *Nephila* secondarily lost it.

Since secondary loss is unlikely on functional grounds, at least in the case of breaking and reeling (above), the more likely monophyletic account is that the ancestor lacked this behavior. This in turn would imply that if orbs are monophyletic, breaking and reeling was acquired independently by both uloborids and non-nephiline araneoids. In each line the behavior would then have revolutionized orb construction, being incorporated into exploration, radius and frame construction, and perhaps in hub removal in somewhat different ways.

This evolutionary sequence is relatively similar to the alternative, polyphyletic hypothesis in having major parts of orb construction evolving convergently. In sum, the observations here imply that even if all orb weavers are descended from an orb-weaving ancestor (more data are needed on this point—Shear 1986), some major aspects of orb construction behavior appear to have arisen independently in different evolutionary lines.

ACKNOWLEDGMENTS

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